

## A GASTROPOD COLOR POLYMORPHISM: ONE ADAPTIVE STRATEGY OF PHENOTYPIC VARIATION

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Most species of the genus *Crepidula* possess very few discrete, multistate traits, but rather show subtle gradations in characters. There are actually very few characters in which polymorphism can be observed, because ornamentation is lacking in most species, and shell shape is a plastic character, strongly affected by the shape of the substrate. However, *Crepidula convexa* does show distinct, nonintergrading color differences within single populations.

The external colors of many species of *Crepidula* are often obscured by algal growth, as well as by a shaggy periostracum. *C. convexa*, however, has a thin periostracum of the same hue as the shell. Being small and able to move, at least in the male phase, it does not become encrusted by advancing colonies of epibionts (bryozoans, algae, tunicates) as do other species. It is photopositive and prefers the upper surfaces of substrates (personal observation), hence its color is visible to other organisms.

The limpet-like *C. convexa* requires smooth, hard substrates in intertidal to shallow subtidal waters. Such substrates—especially the inner surfaces of other shells, polished slate or quartz stones, glass, or, if nothing else exists, eel grass blades—exist in spatially heterogeneous patches. They are also impermanent in time but not usually within the generation time of individual *C. convexa*.

The most common color of the shell of this northern Atlantic species is purplish-grey, with a rich, dark brown interior. Darker rays of pigment extend radially from the apex but are visible only at the shell margin where the background color is less intense. A small proportion of pale tan or yellow shells, with reddish-brown rays, coexists with the darker specimens. An even smaller number of light brown specimens with uneven pigmentation (streaks of yellow mixing with the brown) is usually present. Franz and Hendler (1970) noted these color differences, along with the fact that there were more pale shells living on cultch (clam shell debris) than on gastropod shells. Color differences are discrete, with scoring relatively uncomplicated by ambiguous intermediates.

Color polymorphism in *C. convexa* is of interest because it is a rare occurrence in the genus. Analyses of shell color, substrate color, and relative fitness of individuals of each color on each substrate were performed to investigate how such a polymorphism is maintained in this species. *C. convexa* was compared with one other species which shows discrete color classes, and with species lacking color polymorphism to investigate why it exists in this but not most other species of *Crepidula*.

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MATERIALS AND METHODS

The color, sex, and size (length and height, in mm) of each specimen found in two populations of *C. convexa* were recorded as part of a sampling program during the summer of 1973. The type and color of the substrate on which each snail rested were also recorded. Colors were observed while specimens and substrates were wet. One population was located in the vicinity of the Woods Hole Yacht Club near Penzance Point, Woods Hole, Massachusetts. The other was in Waquoit Bay, Massachusetts. Both populations extended from the lower intertidal zone to three feet below the low tide line. The substrates consisted of small stones, clam and other mollusc shells, scattered eel grass, and trash (glass, porcelain, and cans) on a sandy bottom in the case of the Woods Hole locality, and a mud bottom at Waquoit Bay.

The data were analyzed by means of Chi-square tests to see if shell color correlated with substrate color, or with size or sex. An analysis of the polymorphism in *C. convexa* in light of the fitness-set theory developed by Levins (1968) and applied by McNaughton (1970) and Childress (1972) was conducted. This involved finding a measure of fitness and plotting it for a series of phenotypes (colors) on one substrate *versus* fitness of the same phenotypes on a second substrate. This plot is called a fitness set. Finally, motility of adults and juveniles, sources of predation, and substrates available within the geographical range of the populations studied were observed and recorded for *C. convexa*. The shape of the fitness set was then evaluated in the context of these several ecological factors to

TABLE I  
*Color polymorphism in Crepidula convexa.*

Population	Substrate	Color	Color of <i>C. convexa</i>			Total
			Purple	Brown	Tan	
Woods Hole July, 1973	<i>Littorina</i> Porcelain	brown to purple	108	2	6	116
		white to tan	64	2	10	76
	Total numbers:		172	4	16	192
	Per cent:		89.6%	2.1%	8.3%	100%
Woods Hole Sept., 1973	<i>Littorina</i>	brown to purple	75	7	7	89
	Glass	brown or green	104	6	4	114
	Porcelain	white	8	1	4	13
	Clam shells	white or greyish	9	1	2	12
	Total numbers:		196	15	17	228
Per cent:		85.9%	6.6%	7.5%	100%	
Waquoit Bay Sept., 1973	Eel grass	covered with tan epiphyte	32	3	16	51
		<i>Nassarius</i>	dark purple	9	0	1
	<i>Littorina</i>	brown to purple	33	1	3	37
	Clam shells	white or grey	35	3	11	49
	Stones	white (quartz), some dark	49	2	13	64
	<i>C. fornicata</i>	reddish brown	25	5	6	36
	Total numbers:		183	14	50	247
Per cent:		74.1%	5.6%	20.2%	100%	

determine whether or not the observed color polymorphism could be stable in an evolutionary sense.

### RESULTS

Tables I and II summarize the raw data. No significant correlation between the intensity categories of pigmentation and size categories of the specimens was found, using a Chi-square test of independence ( $0.10 < P < 0.25$ ). Thus, intensity of pigmentation is not a function of age. The largest five individuals, three purple and two tan, were found on white substrates. This is probably a consequence of *C. convexa* growing to larger dimensions on flat surfaces, which coincidentally tend to be of light shade in the localities studied. Large specimens (the females) were better matched to their substrates in intensity of pigmentation than juveniles (Table II). Individuals were uniform in color.

Table I clearly shows that there are far fewer of the intermediate class (brown color) than predicted by the Hardy-Weinberg ratio, under one possible hypothesis—the simplest and most convenient assumption in lieu of breeding tests—that the color system is controlled at one locus by two alleles, with the intermediate color equivalent to the heterozygous class. This assumption is supported by the discreteness of the color morphs.

Table III shows that the color of the shell is not independent of the color of the substrate. There is a higher percentage of tan animals on light backgrounds and of dark animals on dark backgrounds than expected by random distribution. In both the Waquoit Bay and the Woods Hole populations, the association of shell shade with substrate shade deviates significantly from randomness at the 0.005 level. The overall percentage of tan *versus* purple shells differs in the two populations but is constant in two samplings of the same population at a two-month interval (Table I). There are proportionally more tan shells in the Waquoit population, which has the greater percentage of light substrates (about 60% of the exposed surface area in randomly sampled quadrats) than in the Woods Hole population, where 75% of the available substrate is dark. The percentages of intermediate-colored substrates at both Woods Hole and Waquoit Bay are 10%; at Woods Hole these substrates are virtually unoccupied by *C. convexa*. The densities of

TABLE II

*Color matching of C. convexa and substrate by size and sex (J = juvenile; M = male; I = intermediate, changing sex from male to female; F = female). Individuals of the Waquoit Bay and Woods Hole populations have been pooled for this analysis. A match consists of a light snail on a light background, or a dark snail on a dark background.*

Sex	L (mm)	Matched	Mismatched	Percentage matched
J	>0-3	82	90	0.48
M	>3-6	121	51	0.70
M, I, F	>6-9	63	41	0.61
F	>9-12	118	45	0.72
F	>12-15	40	16	0.71
Total		424	243	0.64

TABLE III

Independence test of the color of the snail shell versus shade of the substrate ( $O$  = number observed;  $E$  = number expected under the null hypothesis that the color of the snail shell is independent of the color of the substrate.

A. Waquoit population ( $\chi^2 = 34.2; P < 0.005$ )										
Substrate (Percentage of surface area)	Snail shell color									Total
	Purple			Brown			Tan			
	O	E	$\chi^2$	O	E	$\chi^2$	O	E	$\chi^2$	
Light (60%)	77	93	2.8	8	7	0.1	40	25	9.0	125
Neutral (10%)	25	27	0.2	5	2	4.5	6	7	0.1	36
Dark (30%)	81	64	4.5	1	5	3.2	4	17	9.9	86
Total	183			14			50			247

B. Woods Hole population, two samples pooled ( $\chi^2 = 11.8; P < 0.005$ )										
Substrate	O	E	$\chi^2$	O	E	$\chi^2$	O	E	$\chi^2$	Total
Light (15%)	81	89	0.7	4	5	0.2	16	8	8.0	101
Dark (75%)	287	280	0.2	15	14	0.1	17	25	2.6	319
Total	368			19			33			420

shells on dark and light substrates are similar, showing that *C. convexa* does not preferentially occupy either dark or light substrates. However, there are fewer shells on intermediate substrate shades.

Chi-square values of each substrate calculated independently (1 d.f.) are shown in Table III, in addition to the summed Chi-square value for all comparisons. Most of the individual results are significant, and in the case of the Waquoit population, reveal that the least significant values are for adjacent color combinations (purple shells on neutral substrate, brown shells on light substrate, and tan shells on neutral substrate) as opposed to dark shells on light substrates.

Despite the fact that the gene frequencies in the populations studied here may not be in equilibrium with the immediate environment and it is therefore not possible to conclude that the polymorphism observed is stable, the question of whether or not a balanced polymorphism *could* exist in *C. convexa* is worth pursuing. Application of the data to fitness sets (Levins, 1968) gives insights into why other species of *Crepidula* with different life history patterns should not favor polymorphism. But only if balanced polymorphism in *C. convexa* is assumed may the data be used as a true test of the model. Conversely, to test the possibility of balanced polymorphism, the validity of the model must not be in question. For the present, one can only say whether or not Levins' model is consistent with data on polymorphism in *C. convexa*. It is important that field data be applied to models such as Levins', to increase the dialogue between theoretical and field ecologists.

If the plot of the fitnesses of an ordered series of phenotypes in one environment ( $W_1$ ) versus the fitnesses of the same phenotypes in another environment

( $W_2$ ) is concave in the region between the maximum fitness value in each of the two environments, and if the environments are coarse-grained with respect to the organism, then Levins predicts that polymorphism will be the optimal population strategy. Applying the theory to *C. convexa*, first an estimate of fitness is needed. Clutch size is one means, but is highly dependent on age and size of the female, since these snails continue to grow past maturity and clutch size is proportional to size of the female. The factor most important in individual reproductive success, and hence in estimating fitness of the genotype, is the life span of the individual. In the populations studied, the two "environments" were the dark and the light substrates. They did not differ in food availability to these filter-feeders, or in major physical factors such as temperature, so any differential in size was assumed to be a function of age, not nutrition. This was verified by observing that the distance between major growth lines representing winter growth cessation was similar in equal-sized snails from different substrates in the same population ( $P > 0.5$ ).

Because fitness of the genotype of any individual based upon its life span cannot be obtained by instantaneous measurement, a modified estimator of fitness was used. This was the relative fitness for a group of animals, obtained by finding the mean size of females of each color on each substrate. This produced estimates of differential survival and hence differential reproductive success of the three color morphs of *C. convexa* on each of the substrate "environments." This method assumes a constant yearly recruitment rate and stable age distribution, which are borne out by field studies of recruitment as well as population age and size structure of *C. convexa* (Hoagland, 1975). Such assumptions are invalid for species of *Crepidula* with planktonic larvae, such as *C. fornicata*. Another important assumption is that once mature, females are sedentary and are henceforth subjected to selection pressures particular to the substrate on which they are found.

Table IV gives the results of this analysis, taking into consideration the mass as well as the length of the shell in the estimate of size. Length is a biased estimator of size because some of the dark substrates (*Nassarius* and *Littorina* shells, primarily) are highly convex surfaces, and snails living on them grow proportionally taller than do those on the light substrates (primary clam shells and pieces of porcelain). Records of length and dry weight for a series of 50 individuals from each habitat showed a 10% greater biomass in snails of a given length living on *Nassarius* and *Littorina*, relative to those living on stones and clams. Therefore the lengths of snails living on these substrates were cor-

TABLE IV  
*Differential survival of C. convexa on two colors of substrate.*

<i>C. convexa</i> Shell pigmentation	Mean length in millimeters		
	Light substrate	Dark substrate	Dark substrate, corrected length
Purple	9.5 ± .2*	10.1	11.1 ± .3
Brown	9.8 ± .3	9.3	10.2 ± .3
Tan	11.5 ± .4	8.9	9.8 ± .2

\* Mean ± standard error.



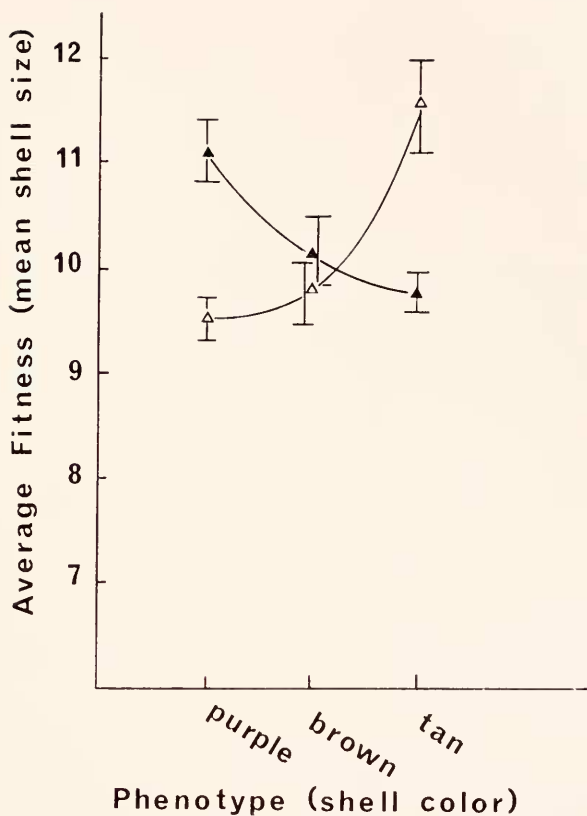


FIGURE 1. Average fitness as a function of phenotype of *Crepidula convexa* in two environments. Fitness is estimated as mean shell length for all female individuals of each color on each substrate (environment). Vertical bars are one standard error unit. Open triangles represent light substrates; and solid triangles, dark substrates.

rected by multiplying them by a factor of 1.1 (last column of Table IV). Figure 1 is a plot of the phenotype (color) *versus* average fitness (survival, as measured by shell size), for the two environments. Figure 2 is a plot of the resulting fitness set, for the critical region between  $W_1$  (max) and  $W_2$  (max). It shows that, indeed, the fitness set is concave. This is because the survival of the intermediate phenotype, the brown shells, is low on both dark and light substrates. In the terminology of this paper, it makes a "mismatch" on either substrate. The heavy mortality of this poorly-adapted heterozygote represents the cost of the strategy of polymorphism to *C. convexa*; it must be outweighed by the fitness of the two extreme color morphs in the heterogeneous environment in order for polymorphism to be a viable strategy. The sedentary females have higher survival on matched substrates.

General ecological observations complement the fitness set analysis. Records of species living in Vineyard Sound (Verrill and Smith, 1874) reveal that the intertidal to shallow-water populations of *C. convexa* are not isolated but are in

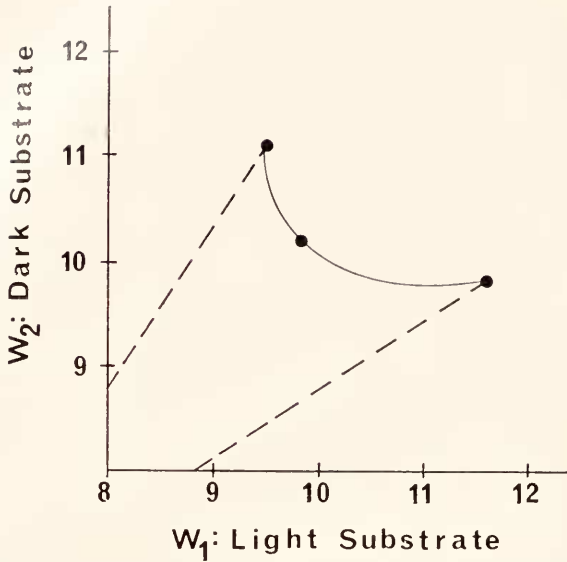


FIGURE 2. A fitness set for *Crepidula convexa* on two substrates. The points represent the three color morphs (purple, brown, and tan) from left to right. The X coordinates ( $W_1$ ) are the mean lengths of each morph on light substrate; the Y coordinates ( $W_2$ ) are the mean lengths of each morph on dark substrates.

communication with deeper-water populations and probably also those of other shallow water areas. The demes are separated by unsuitable substrate (sand), but individuals are transported by plant and animal hosts, as demonstrated by the discovery of young *C. convexa* on fragments of eel grass and especially on horseshoe crabs and hermit crabs which migrate to deeper waters in winter. Gene flow is probably high enough to maintain an unbalanced polymorphism without speciation, evidence for which is present in over one hundred years of shell specimens from the New England area now housed in American museums (Academy of Natural Sciences, Philadelphia; Museum of Comparative Zoology).

One seemingly anomalous fact is that there are available to most populations of *C. convexa* not only black and white stones and shells, but grey stones as well, usually mottled granites. Juvenile individuals of *C. convexa* occasionally settle on these, but very few adults are ever found on them. Rocks of mixed or intermediate shades are usually of heterogeneous composition and are rough in texture, for they erode unevenly. Individuals of *C. convexa* avoid these in favor of smooth substrates, as seen by placing specimens of *C. convexa* in laboratory tanks with various substrates available to them. Thus, there is a dichotomy of substrate shades available to *C. convexa* in the sites studied, despite the presence of other shades in the environment.

It is important in evaluating the stability of the color polymorphism to know how free *C. convexa* is to move from one substrate to another. Motility of *C. convexa* was observed in the field and in laboratory tanks. Both males and females showed high motility during the first one to two days after placement of

50 individuals of each sex in a laboratory tank. If smooth substrates were available, females became stationary after the initial one to two day period. If tank conditions were altered to increase water temperature or to reduce the amount of oxygen in the water, *C. convexa* females became motile again, unless they were brooding young. Brooding females were completely sedentary. Males became stationary on females for periods ranging from a few hours to 29 days, most frequently 20 days. After such a stationary period, a male either separated from the female and changed sex, or found another female.

In the field, marked individuals of *C. convexa* were difficult to recover because their substrates were either living and moving themselves, or were moved by tides and currents. Young individuals (less than 5 mm long) of *C. convexa* appeared to be highly motile, but brooding females were sedentary and some males were associated with females for periods as long as two months.

To see if shell color could directly affect mortality of individual *C. convexa* and hence be strongly controlled by natural selection, possible causes of mortality were examined. No specimens of *C. convexa* were found which had been drilled by gastropod predators. Starfish were never seen attacking *C. convexa* or the *Nassarius* or *Littorina* on which they lived, though starfish were found on nearby mussel beds. Crabs were frequently observed eating *C. convexa* and young *Littorina littorea*. Once a gull was seen smashing the shell of a *L. littorea* which had two *C. convexa* attached to it. These observations indicate that visual predators which could detect pigment differences (crabs and birds) might be important in killing *C. convexa*, while primarily olfactory predators such as starfish and drilling gastropods are probably less important.

#### DISCUSSION

Several assumptions have been used in interpreting the data so far presented. The most critical is that pigmentation is a genetic character basically unchanged by the environment, and constant throughout the lifetime of any individual. Moore (1936) suggested that diet plays a large role in the color variation of *Purpura* (= *Nucella*) *lapillus*. However, because all species of *Crepidula* are filter-feeders, their diets are less likely to be the cause of cryptic coloration than those in animals that feed directly on the substrate they occupy. The fact that no individuals of *C. convexa* were found which changed color in mid-growth is consistent with the assumption. Also, the assumption that a genetically controlled color system is controlled at one locus is compatible with the genetic bases of other molluscan color polymorphisms (Cain and Sheppard, 1950, 1954; see also Komai and Emura, 1955). However, the exact genetic mechanism is not critical to the argument developed below.

One might ask if the color morphs of *C. convexa* are really different species. The possibility is discounted by the presence of intermediates, male-female pairings between the morphs in the laboratory (such pairings do not occur between species), simultaneous breeding times, identical larvae, identical morphologies other than color, and by similar maximum size and lifespan.

Incipient speciation through geographical isolation is an unlikely explanation for discrete color morphs, but is hard to disprove without direct evidence on gene flow and gene frequencies over time. However, *C. convexa* is identifiable in the



fossil record from the mid-Miocene to the present, with a range from Nova Scotia to Western Florida, without the development of species complexes of closely related forms such as occurs in *Littorina* (Borkowski and Borkowski, 1969).

Taking the body of fact and assumptions presented, it appears that selection is operating to reduce the numbers of the intermediate color type and to favor dark over light shells in *C. convexa* on dark backgrounds. Benefit also accrues to light shells on light backgrounds. Either the snails are able to find a substrate of matching color, or predation causes a reduction in the number of mismatched snails, or both. Because larger specimens of *C. convexa* were better matched to the background color than younger and smaller specimens, predation could be acting to weed out mismatched individuals. The lower percentage of matched snails at the length range of six to nine mm (Table II) is due to the intermediate sexual stage occurring at about that size. The animals change substrates at the time of their sex change to female, because they then move off their mates and appear to be repelled by them. They again must sort themselves out as to color background, possibly through a behavioral mechanism. The behavioral mechanism is unknown and its existence unproven. Such a mechanism was hypothesized by Giesel (1970) to explain the matching of *Acmaea digitalis* to its substrate, but that case is complicated by homing behavior in the adult limpets (Fretter and Graham, 1962, p. 498). *C. convexa* does not home.

Opposite proportions of dark and light substrate in neighboring localities could affect the gene frequencies by creating selection pressures favoring different colors of *C. convexa* in different places, with some mixing occurring due to the transportation of adults. Additionally, the subtidal portion of each *C. convexa* population may not be under the same intensity of visual predation as that portion which is intertidal. The behavioral trait of being able to match shell shade to substrate, if it exists, would have a stabilizing effect on the color polymorphism in any one population. It would be of interest to study an isolated population of *C. convexa* where gene flow to and from other populations is very low, to see if one or the other pigment shade became fixed, or if the polymorphism could be balanced.

The concave fitness set resulting from the plot of fitnesses of different shell colors on light and dark substrates is compatible with the hypothesis that color polymorphism in *C. convexa* is balanced. Levins' fitness set model for balanced polymorphism further requires that the environments be "coarse-grained" with respect to the organism in order for polymorphism to evolve. An organism is coarse-grained if it spends disproportionate time in one of several temporally or spatially arranged habitat patches within a heterogeneous environment (Gillespie, 1974; Maynard Smith, 1970; Levins, 1968; Levene, 1953). The limited mobility of *C. convexa*, combined with its small size relative to the habitat patches (rocks, shells, and sand), its brooded (nonplanktonic) young, and its hypothesized ability to choose a substrate befitting it, makes it coarse-grained with respect to the spatial environment. This completes the criteria necessary and sufficient for *C. convexa* to possess balanced color polymorphism. An individual *C. convexa* may spend a major portion of its lifetime in one of several contemporaneous habitat patches, while its offspring may spend their lifetimes in different patches.

Therefore, it is possible that *C. convexa* can maintain a color polymorphism without genetic exchange between populations. However, the proximity of other

habitats with different proportions of substrate types and potential predators to the populations studied, as well as a means for individuals to migrate between the habitat areas, suggests the possibility of polymorphism based on genetic exchange within the Woods Hole area.

*C. convexa* is unable to accommodate ice scour, occurring every three to seven years in the cold temperate marine intertidal zone. This is due to the short lifespan of the individual and marks it as coarse-grained with respect to time. However, this factor is probably not relevant to color polymorphism, unless the severe weather were to coincide with substrate disruption, which does not happen in the localities studied. Temporal environmental fluctuations might be expected to cause polymorphism in metabolic characters.

Looking at other members of the genus *Crepidula*, *C. adunca* is the only one which shows color polymorphism. This Pacific species is ecologically similar to *C. convexa*. It is chocolate brown or yellow, with very little representation of intermediate shades. As with *C. convexa*, the question is one of intensity of pigmentation rather than presence of different colors. Populations in Monterey, California, contain a high proportion of dark shells, while some from Southern California are primarily yellow. Some populations are entirely one color or the other (personal observation). Besides predation, pigmentation of intertidal gastropod shells may be a factor in regulating heat absorption during exposure at low tide. Darker shells absorb more heat and may be disadvantaged in southern climates. Furthermore, the percentage of dark backgrounds in Monterey is over 50%, while it is less than 50% in most Southern and Baja California localities, suggesting that the predominant color of *C. adunca* may be due to camouflage.

A conflicting adaptive context would exist if a population had to cope with a hot environment, while the majority of substrates were dark. The strategy for camouflage (dark color) would conflict with the strategy for heat loss (light color). An interesting test of the importance of heat loss *versus* camouflage could be undertaken if specimens of *C. adunca* were found living on predominantly dark substrates in the southern part of its range. Examination of such a population would give insight into the dominant selective pressure for color polymorphism in this species.

Unique conditions relevant to color polymorphism shared by *C. convexa* and *C. adunca* are that their inherited shell color is usually not obscured by epibionts, they frequent the intertidal zone particularly by attaching themselves to the shells of intertidal gastropods, and they are subject to predation by gulls, shore birds, and crabs more consistently than by starfish and predatory gastropods, according to field observations and laboratory tests (Hoagland, 1974). All visual predators attack all size classes, probably because the range of size within these species is small (1–20 mm). Birds and crabs are visual predators, whereas starfish and gastropods such as *Urosalpinx* and *Thais* rely more on olfactory stimuli (Owen, 1966, pp. 23–25; Carriker, 1955). Strictly subtidal species of *Crepidula* do not exhibit color polymorphism (Hoagland, 1977). They are heavily preyed upon by olfactory predators such as starfish. However, the reason for the difference in types of predators is only partly the vertical position of the *Crepidula* on the shoreline. Size of the individuals and population density are important factors. Starfish and drilling gastropods have definite hierarchical prey preferences (Paine, 1969), and

they virtually ignore the small and relatively rare *C. convexa* and *C. adunca* during the feeding periods of these predators. They prefer mussels, the larger and more numerous sympatric species of *Crepidula* (*C. onyx* in the Pacific and *C. fornicata* in the Atlantic), or barnacles, in the case of *Urosalpinx* in the intertidal zone at Woods Hole (Hoagland, 1974).

The small intertidal species of *Crepidula* lack a planktonic larval stage and live for only two to four years, compared with an estimated maximum life span of eight to ten years for the larger *Crepidula* species (Hoagland, 1975). Perception of environmental heterogeneity therefore must differ for individuals in the two groups of species. For example, *C. fornicata* has low mobility, but appears to be fine-grained in its choice of substrates. In the laboratory, it does not distinguish substrates on the basis of micro-texture. It settles on exposed and sheltered surfaces, horizontal and vertical. This is one of several characters by which it may be termed a generalist—temperature and salinity tolerance are others. The significance of the generalist mode is that it, along with the planktonic larval form, enables individuals of *C. fornicata* to excel in establishing themselves in new areas. Their longer life span relative to *C. convexa* means that adaptation to cyclical environmental heterogeneity is possible and desirable. If the range of the environment is less than the tolerance of individual phenotypes, a convex fitness set should result. One could predict, on the basis of grain size, low polymorphism. There is no evidence of visually detectible polymorphism in *C. fornicata* or any ecologically similar species (*C. onyx*; *C. dilatata*), but rather there is phenotypic plasticity, a strong molding of each individual by its immediate environment.

Following the lines of this argument, species with homogenous habitats are not expected to have either high polymorphism or plasticity. Species with low visual predation are unlikely to possess color polymorphism. *C. plana* and other photonegative *Crepidula* fall into this category. Their habitat preferences are narrowly defined, restricted to the under- or inner-surfaces of solid objects. *C. plana* is primarily subtidal, except when it lives on the undersides of living organisms where it is continually kept moist and is not readily visible to sight predators. Therefore, selective pressure for color matching with the substrate is not a significant factor in the biology of *C. plana*.

Balanced polymorphism is an alternative to phenotypic plasticity, in that both strategies allow a population, on a statistical basis, to broaden its niche (to extend over a diversity of substrates) when occupying a habitat which is unpredictably heterogeneous in space or time. In the genus *Crepidula*, expression of color polymorphism is related to spatial heterogeneity. Its presence depends upon the particular species' lifespan, mobility, substrate preferences, and mode of major predators' attack. In *C. convexa*, each of two color morphs is superior on a particular substrate, while intermediate forms are less successful.

Other polymorphic characters, such as enzymes, might be expected to be found in *C. convexa* and *C. adunca* populations as a result of temporal heterogeneity of their environments. Polymorphism is the favored strategy when, as with *C. convexa*, environmental fluctuations occur over a time span equal to or slightly longer than the lifespan of the organism, or when the organism is relatively sedentary in a heterogeneous environment and different selection pressures operate in different environmental patches. Short-term environmental fluctuations rela-

tive to the lifespan of the organism, or high mobility of an animal within a heterogeneous environment, or lack of discrimination between patches, favor phenotypic plasticity. Narrow habitat preferences correlate with specialized behavioral and morphological characteristics, and with the lack of either color polymorphism or phenotypic plasticity.

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#### SUMMARY

A case of shell color polymorphism in the shallow water mesogastropod *Crepidula convexa* is described. Polymorphism of color in *C. convexa* appears to be based on disruptive selection, which occurs due to the availability of two contrasting shades of substrate, heterogeneous in time and space, combined with mortality from visual predators.

Data on the relative survival of the two phenotypes of *C. convexa* in two patches of a heterogeneous environment are applied to the fitness set model developed by Levins (1968). The necessary and sufficient criteria for a stable polymorphism are met, but reasons are set forth for believing that this is, rather, a case of unstable polymorphism.

Only one other species of the genus, *C. adunca*, shows a similar color polymorphism. Ecological factors uniquely shared by the two species are: visibility of inherited shell color, a major part of the population living in the intertidal zone, and an impact by visual predators. Color polymorphism is correlated with visual predation on a heterogeneous substrate, and with low adult mobility. In general, the strategy of polymorphism is advantageous to some species of *Crepidula* and not others, depending on heterogeneity of the environment in time and space, with respect to its use by the organisms.

Other patterns of phenotypic variation found in *Crepidula* are phenotypic plasticity and phenotypic uniformity. Uniformity occurs when a species' behavior pattern restricts it to homogeneous environments. Plasticity, like polymorphism, increases niche size in heterogeneous environments; plasticity is favored when each organism must cope with environmental change within its lifetime. These patterns of natural selection for phenotypic variation probably apply to a wide variety of organisms.

#### LITERATURE CITED

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